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## ECOLOGICAL ASPECTS OF THE DISTRIBUTION OF SUBSOIL HERPETOFAUNA IN NDUMU GAME RESERVE

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### INTRODUCTION

The tropics are inhabited by numerous species of fossorial squamates, many of which show limb reduction. Most of the papers dealing with these refer to taxonomy or morphology, and relatively little is known regarding the factors influencing their distribution (Gans, 1968, 1971). The lack of such data is even more important in view of the rapid and sweeping ecological changes now occurring in many tropical areas. For this reason, the generation of preliminary ecological data was one of the aims of a survey trip (by Gans) to various African localities during 1969. (Gans completed work for his contribution to this paper while associated with the Department of Biology, State University of New York at Buffalo.)

The data presented here were obtained by A. C. Pooley in the Ndumu Game Reserve as a byproduct of an intensive program of collecting the amphisbaenian *Zygaspis violacea* (cf. Pooley, 1965, 1970 for miscellaneous records on the Ndumu herpetofauna). It is hoped that their availability will stimulate more intensive and extensive surveys of other areas.

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## METHODS

All the surveys were carried out in Ndumu Game Reserve and adjacent area, in Zululand, South Africa, a locality that lies on an effective temperature line between  $17^{\circ}$  and  $18^{\circ}$  on Stuckenberg's (1969) map. The area receives approximately 700 mm of rainfall annually (Nuttonson, 1961), most of it falling from January through March (see South African Weather Bureau Publications 19, 22, 28, and 29 for more detailed climatological data). The seasonal climatic pattern of the area is influenced not only by rainfall changes, but also by the flooding of the Pongola River which fills the large pans adjacent to this area, usually during January to March. The study areas tend to be flooded intermittently at that time. This flooding pattern has now been interrupted by the construction of the J. G. Strydom Dam.

Ndumu, the only hill in the area, rises to 573 feet above sea level. Reports indicate that it is composed of red sands (Ibumdu) overlying Cretaceous strata at the base. The red sands contain much magnetite, and their grains are rounded and covered by some form of haematite, possibly indicating aeolian origin (K. L. Tinley, MS).

Four major habitats were sampled to a total of 524 square yards. All sample plots were dug to a standard depth of 2'6", since previous collections have revealed no reptiles at greater depths. The collections reported here were assembled during March and April, 1970, except for the Group D excavation, which was made as a byproduct of construction work for crocodile pens.

## DESCRIPTION OF AREAS

### HABITAT GROUP A

The plots sampled were located on the Ndumu hill at elevations between 200 and 400 feet above sea level. A total of 496 square yards was sampled (fig. 1).

PLOT A.1: This plot included 360 square yards of firmly packed orange-red, fine sand. It included three vegetation types, each with an area of 120 square yards. These are referred to as subplots A.1.a, A.1.b, and A.1.c.

SUBPLOT A.1.a: This area was covered by sparse grasses, occasionally occurring in mats but with intermediate areas of exposed soil. Tufts of the grasses *Trichoneura grandiglumis*, *Pogonarthria squarrosa*, *Aristida congesta*, and *Aristida congesta barbicollis* were 9 to 30 inches tall. The soil was dry to a depth of 18 inches and contained clumps of tangled grass roots. Invertebrates were abundant at the surface but were uncommon underground.

SUBPLOT A.1.B: A three-story canopy kept this area well shaded with little or no direct sunlight reaching the surface (Figure 2). The



Fig. 1. Ndumu hill habitat in which Group A plots were located. This was the only area in which *Bufo regularis* was taken.



Fig. 2. The A.1.b subplot after digging. It is still heavily shaded even though much of the understory vegetation was removed during the collecting.

ground cover was composed of the grasses *Trichoneura*, *Pogonarthria*, and *Aristida* and scattered small shrubs including *Maytenus senegalensis*, *Securinega virosa*, *Eugenia* sp., *Rhus guenzii*, *Euclea crispa*, and *Aloe marlothii*. The intermediate canopy was small trees reaching a height of 8 to 12 feet. These were *Vangueria cyanescens*, *Strychnos spinosa*, *Terminalia sericea*, *Boscia filipes*, *Dichrostachys cinerea*, and *Commiphora neglecta*. The upper canopy was a *Sclerocarya caffra* of up to 30 feet. The soil surface was covered by decomposing fruits of *Sclerocarya caffra*, leaf litter, and fragments of bark and twigs. The soil contained numerous roots but little other organic matter, and was damp to within 6 to 12 inches of the surface. Invertebrates were abundant throughout.

SUBPLOT A.1.C: This subplot had a discontinuous ground cover of the grasses *Trichoneura*, *Pogonarthria*, and *Aristida*. Some shading was provided by *Strychnos spinosa*, *Terminalia sericea*, and *Dichrostachys glomerata* up to 10 feet tall. The soil was dry to a depth of 15 to 18 inches, and contained clumps of matted grass roots, but few invertebrates.

PLOT A.2: This plot had an area of 55 square yards with red-brown soil rich in organic matter. It contained a single *Boscia* sp. 10 feet tall, *Aloe marlothii*, and isolated clumps of the grasses *Aristida* sp. and *Trichoneura* sp. The ground was covered by a 6-to-12-inch layer of decomposing plant material. There was abundant moisture at all depths and many invertebrates were present.

PLOT A.3: The plot consisted of 36 square yards of red-brown soil covered by a continuous layer of grasses (Figure 3). It was partly shaded by two *Kigelia pinata* 25 feet tall. The soil was dry to depths of 18 to 24 inches, and had clumps of grass roots and few invertebrates.

PLOT A.4: This area of 45 square yards of dark brown-gray soil was covered by a 2-foot layer of dried grass atop 6 inches of humus (Figure 4). The soil was loose, damp at all depths, and invertebrates were very abundant.

#### HABITAT GROUP B

The plots sampled were on the eastern slope of Ndumu hill bordering Khondo forest at an altitude of about 100 feet. The area is a sand forest bordering formerly cultivated fields. The ground cover in the forest included the shrubs *Salacia leptoclada*, *Vitex patula*, *Crassula* sp., *Jatropha variifolia*, *Sansevieria grandis*, *Senecio fulgens*, *Stylochiton natalense*, and *Ornithogalum virens*.

The soil surface was variously covered with both open and densely vegetated areas. The subordinate canopy was composed of 5-to-15-foot tall specimens of *Boscia longipedicillata*, *Wrightia natalensis*, and *Drypetes arguta*. The upper story of 15-30 foot trees included





Fig. 3. Plot A.3 after digging was completed. The trees in the foreground are *Kigelia pinata* that partially shaded the collecting site.



Fig. 4. The site of plot A.4. The remnants of dried grasses in the foreground originally covered the entire plot.

*Cleistanthus schlechteri*, *Pteleopsis myrtifolia*, *Brachylaena huillensis*, *Croton gratissimus*, and *Newtonia hildebrandtii*, which was the dominant species. The soil was fine, gray-white and contained some humus. All plots were 2 yards square.

PLOT B.1: This plot was in a densely shaded portion of the forest and was covered by a layer of leaf litter (Figure 5). The soil was moist to within 3 inches of the surface and contained many roots, bulbs, and invertebrates.

PLOT B.2: The plot was similar to B.1.

PLOT B.3: This plot lay at the base of a large specimen of *Albizia petersiana* ssp. *evansii* that was on the interface between forest and field. The plot was lightly shaded with a few clumps of small plants. The soil was fine, grayish-white in color. It was rich in organic matter, moist to within 3 inches of the surface but dry at the surface. Invertebrates were abundant.

PLOTS B.4 AND B.5: These plots were similar to B.3.

PLOT B.6: Specimens were collected from an area of short grass tufts at the edge of the forest. The soil was loose, moist below 3 inches, and had few invertebrates.

#### HABITAT GROUP C

These plots (2 square yards in area) were in old cultivated fields adjacent to the forest habitat in Group B (Figure 6). The area was formerly sand forest, and a few trees, e.g., *Sclerocarya caffra*, *Trichelia emetica*, *Acacia nilotica*, and *Gardenia cornuta* remained. A few *Maytenus heterophylla* bushes were present. The soil varied in color and texture, owing to erosion and repeated plowing. Subsoil invertebrates were uncommon.

PLOT C.1: This plot was in the center of an old field. Isolated tufts of grass were present. The orangish, fine, sandy soil was covered by leaf litter and twigs. Little organic matter was present and no invertebrates were observed.

PLOT C.2: This plot included an unused termite mound 3 feet tall. The mound was covered by *Azima tetracantha*. The mound was hard and dry at the surface but moist at a depth of 12 inches. The soil was orange-yellow, soft around the base of the mound, and rich in humus. No invertebrates were noted.

PLOT C.3: A plot at the base of a *Sclerocarya caffra* was sampled. It was lightly shaded and covered by a sparse layer of leaves and twigs. The soil was orange-yellow, dry at the surface, but moist at a depth of 12 inches. Few invertebrates were found.

Fig. 5. Site of plot B.1 after digging. A densely shaded area in the sand forest.

Fig. 6. View of old field area where Group C collections were made. Very few specimens were taken here.





PLOTS C.4 AND C.5: These plots were similar to C.3.

PLOT C.6: This plot was at the base of a *Trichelia emetica*, which provided dense shade. There was abundant leaf litter, and the brown soil was moist at all depths and rich in humus and invertebrates.

PLOT C.7: This plot was in the shade of a *Gardenia cornuta*. The area beneath a pile of leaves, grass, and twigs was sampled. Invertebrates were abundant.

PLOT C.8: This plot encompassed a small (1 m high), abandoned termite mound in open grassland. The soil was gray-brown, rich in humus, and contained little moisture. No invertebrates were noted.

#### HABITAT GROUP D

Twenty-six dams or pools were excavated at the base of Ndumu hill, on the edge of the Pongola River floodplain, at an elevation of 90 to 100 feet. The vegetation included the dominant grasses *Chloris virgata* and *Eragrostis cilianensis*, and the shrubs *Hermboetia odorata* and *Hibiscus cannabinus*. There were a few thickets of *Maytenus nemorosus* and some small trees like *Dichrostachys glomerata*, *Acacia nigrescens*, and *Acacia nilotica*. A few large trees, *Trichelia emetica*, *Sclerocarya caffra*, *Kigelia pinata*, provided shade in an otherwise open area. The soil was gray-black clay of extremely dense consistency. There were very few invertebrates.

#### SPECIES ABUNDANCE AND DISTRIBUTION

The species and numbers of individuals collected in 1970 are presented in Table 1. The species composition of the 1969 Ndumu hill collection is in Table 2. Since so few specimens of *Hemidactylus marmoratus* (1), *Xenocalamus transvaalensis* (1), *Aparallactus c. capensis* (1), *Scelotes arenicola* (2), and *Riopa sundevallii* (3) were collected, little may be said about their ecological distribution except that a variety of forms exists in a relatively small area at apparently low-population densities. Whether this reflects generally low incidence of these species in the area because of some adverse environmental factor, results from behavioral traits that cause wide dispersion, or is an artifact of the collecting technique, cannot be determined from these data.

*Bufo regularis* occurred only in Habitat Group A. This species was third in number of individuals collected. Since 7 specimens were taken in the Habitat A area and none in Habitat Groups B and C, it is probable that some environmental factor restricted their distribution.

*Scelotes bidigittatus* and *Zygaspis v. violacea* were by far the most abundant species. They made up 39% and 43%, respectively, and 82% collectively, of all specimens collected. All habitats sampled, with the exception of Group D, were occupied by these species.



TABLE 1. HABITAT

Species	GROUP A							GROUP B						
	A.1.a	A.1.b	A.1.c	A.2	A.3	A.4	Total	B.1	B.2	B.3	B.4	B.5	B.6	Total
<i>Bufo regularis</i>	1	2	0	1	0	3	7	0	0	0	0	0	0	0
<i>Hemisus marmoratum</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Riopa sundevallii</i>	0	2	0	1	0	0	3	0	0	0	0	0	0	0
<i>Scelotes bidigitatus</i>	7	11	2	1	1	3	25	1	0	3	0	1	0	5
<i>Scelotes arenicola</i>	1	1	0	0	0	0	2	0	0	0	0	0	0	0
<i>Zygaspis v. violacea</i>	3	17	1	2	0	2	25	0	1	3	2	1	2	9
<i>Aparallactus c. capensis</i>	0	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Xenocalamus transvaalensis</i>	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Total	12	34	3	6	1	8	64	1	1	7	2	2	2	15
Square Yards	120	120	120	55	36	45	496	2	2	2	2	2	2	12
Animals/Square Yard	.1	.28	.025	.019	.028	.178	.129	.5	.5	3.5	1.0	1.0	1.0	1.25

TABLE 1. HABITAT (continued)

Species	GROUP C								GROUP D		
	C.1	C.2	C.3	C.4	C.5	C.6	C.7	C.8	Total	D	Total
<i>Bufo regularis</i>	0	0	0	0	0	0	0	0	0	0	7
<i>Hemistis marmoratum</i>	0	0	0	0	0	0	0	0	0	0	1
<i>Riopa sundevallii</i>	0	0	0	0	0	0	0	0	0	0	3
<i>Scelotes bidigitatus</i>	0	0	0	0	0	3	0	0	3	0	33
<i>Scelotes arenicola</i>	0	0	0	0	0	0	0	0	0	0	2
<i>Zygaspis v. violacea</i>	0	0	0	0	0	0	2	1	3	0	37
<i>Aparallactus c. capensis</i>	0	0	0	0	0	0	0	0	0	0	1
<i>Xenocalamus transvaalensis</i>	0	0	0	0	0	0	0	0	0	0	1
Total	0	0	0	0	0	3	2	1	6	0	85
Square Yards	2	2	2	2	2	2	2	2	16	?	524
Animals/Square Yard	0	0	0	0	0	1.5	1.0	.5	.375	0	.162

TABLE 2. NUMBERS OF SUBSOIL VERTEBRATES COLLECTED FROM N'DUMUHILL IN 1969.

<i>Scelotes bidigitatus</i>	. . . . .	.40	<i>Xenocalamus transvaalensis</i>	. . . . .	.1
<i>Scelotes arenicola</i>	. . . . .	.14	<i>Leptotyphlops conjuncta</i>	. . . . .	.3
<i>Zygaspis v. violacea</i>	. . . . .	.27	<i>Elapsoides sundevallii decosteri</i>	. . . . .	.1
<i>Riopa sundevallii</i>	. . . . .	.3	<i>Calamellaps unicolor miolensis</i>	. . . . .	.1
<i>Aparallactus c. capensis</i>	. . . . .	.1	<i>Bufo regularis</i>	. . . . .	.7
<i>Atractaspis b. bibroni</i>	. . . . .	.2			

## HABITAT AND ECOLOGICAL FACTORS

Some caution must be applied in the interpretation of Table 1. The principal difficulty lies in comparison of the numbers of animals per square yard. The plots in Group A were much larger than those of Groups B and C. This may have biased the data since smaller plots were likely to be chosen to include optimal habitat areas while the larger plots of Group A contained areas of more varied habitat. Since amphisbaenians are well able to detect the vibrations caused by digging (Gans and Wever, 1972), there is a greater probability of escape from small than from large plots. Hence we have omitted statistical analyses until more comparable samples may be taken.

The relative abundance of invertebrates was the most obvious factor relating to the numbers of vertebrates present in the soil. When invertebrate abundance is categorized as either many or few, plots A.1.a, A.1.b, A.2, A.4, B.1, B.2, B.3, B.4, B.5, C.6, and C.7 had many, while A.1.c, A.3, B.6, C.1, C.2, C.3, C.4, C.5, and C.8 had few. In the 11 plots having many invertebrates, there were 78 vertebrates collected, compared with 7 from the 9 plots with few invertebrates. The number of vertebrates per square yard was .221 for the plots with many invertebrates, and was .041 for the plots with few invertebrates (Group D is omitted from this analysis). The correlation of abundant invertebrates and abundant reptiles does not appear in all the subgroups of A, confirming that other factors are also involved.

The next critical factor appears to be the particle size and packing of the soils (see Collis-George, 1959 for a theoretical discussion of soil environments). The area sampled for Group D was larger than the total of groups of A, B, and C, yet no specimens were collected. While no particle size analyses are available, inspection indicated that the relative proportion of fine, particulate silts is much higher in floodplain deposits than in the other sites. This is a well-known phenomenon reflecting the introduction of fine, particulate matter during flooding and its washing out by rainfall runoff from other areas. Equally important would seem to be the more ready drying and aeration in regions A, B, and C owing to wind action and root penetration.

All areas with high densities of invertebrate and vertebrate faunas represent natural associations. Group C, the old field habitat, had few invertebrates, a poor subsoil herpetofauna, and much tighter soil. This is of interest since certain other species of amphisbaenians, for instance *Amphisbaena schmidtii*, *Amphisbaena caeca* (Gans, 1964), and *Cynisca leucura* (personal observation by Gans), are common in cultivated areas, particularly when the soils are well aerated. There seems to be an increase in invertebrates associated with monoculture. The present observations suggest that the suitability of once-cultivated

areas may rapidly degenerate between the time cultivation ends and the time that natural vegetation is re-established. This could be of particular importance in tropical areas where soils are subject to rapid changes when even temporarily denuded of ground cover.

The effect of temporary flooding either by river water or by rain water should not be underestimated. Various central and east African regions are characterized by pans, localized zones in which the subsoil permeability has been reduced by particulates so that water remains standing for prolonged periods. Such pans attract game animals.

It is well known that when soil suspensions in water are allowed to settle, the largest particles settle first and fine, particulate matter then accumulates, forming a relatively fine-grained surface layer. It is this layer that presumably inhibits aeration in soil. Repeated flooding intensifies this process. Its results in nature may be seen in any small depression with poor drainage. A good example of such particulate stratification was observed (by Gans) along a transect bulldozed during road construction in the Tsavo National Park, Kenya. Each small depression showed the characteristic accumulation of fine, particulate matter as well as marked reduction in number and changes in the species composition of the fossorial vertebrates.

Finally, it might be useful to speculate briefly on the effect of the tunnel systems produced, at least by *Zygaspis*, on aeration and invertebrate distribution. Since the tunnels perforate the soil surface from below, they loosen the compacted layer and allow the finer particulates to drift downward. They serve as passageways for upward dispersion of water vapors. Laboratory observations suggest that they have a consequent attraction for hygrophilic insects. Besides providing access to food sources, they would facilitate vertical movements and act as sources and sinks for water and thermal energy. Unfortunately we still lack maps of even a few tunnel systems.

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